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Habitat drivers of endangered rorqual whales in a highly impacted upwelling region

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ABSTRACT

Recent studies show that human impacts on marine ecosystems are threatening marine biodiversity. A greater emphasis on predicting how predators might respond to changes in the marine environment is needed because the effects of human activities are spatially heterogeneous. Here we analyse rorqual whales distribution data in a highly impacted upwelling region (North-western Iberian coast, Spain). Using a multi-model inference approach this study assesses the habitat drivers of the fine-scale distribution of three endangered whale species (blue, fin and sei whales) as a way to better understand how rorqual whales might respond to human-induced changes in the coastal ecosystem. The unequal use of available habitat, concentrated at the edge of the continental slope (200 m depth and strong bottom slope gradient) in areas with a south-easterly coastal orientation, showed that rorqual whales presented a fine-scale pattern of habitat selection in response to prey availability. Rorqual whales' distribution is affected by the coastal upwelling regime of the Iberian Peninsula, which is known to be under impact of climate change. Therefore, responses of rorqual whales to upwelling changes might be manifested at the population level such as shifts in abundance and distribution. This information contributes to extend the scant information available about the presence of these species in the North-east Atlantic. Our findings provide management agencies with an opportunity to devise and implement adequate adaptation measures which may ameliorate adverse effects critical for the conservation of rorquals in a changing climate.

1. Introduction

Anthropogenically-induced climate change, along with exploitation, fisheries by-catch, habitat modifications, and pollution, are some of the most significant threats to marine biodiversity (Pauly et al., 2005; Harley et al., 2006; Read et al., 2006; Hoegh-Guldberg and Bruno, 2010). The impacts of human activities are causing shifts in the distribution of marine predators, through direct physiological and indirect ecological pathways, and are increasing the likelihood of local extinction (Walther et al., 2002; Butchart et al., 2010). Predicting the biological effects of human-induced changes in the marine ecosystem on marine predators is complex and depends on how individual species respond to local changes in the environment (Harley et al., 2006; Brook et al., 2008; Forcada and Trathan, 2009). Because the effects of human activities are spatially heterogeneous, the intensity of the responses of marine predators to human activities may vary over a species range resulting in some species having a higher vulnerability in specific areas of their range (Trathan et al., 2007; Fuentes et al., 2011). Therefore, understanding the factors that are responsible for the fine-scale distribution of species is fundamental to better understand how these species respond to human-induced changes in their environment.

Whales of the genus Balaenoptera are K-selected, highly migratory, long-lived, marine predators that are under threat from human activity and influenced by climate variability across the world's oceans (Walther et al., 2002; Trathan et al., 2007; Kovacks and Lydersen, 2008). During the last century, most populations were severely depleted by whaling (Rocha et al., 2014) and as a consequence, blue whales (*Balaenoptera musculus*), fin whales (*Balaenoptera physalus*), and sei whales (*Balaenoptera borealis*) are considered among the most threatened cetaceans worldwide (listed as "endangered" in the IUCN red list, Reilly et al., 2008a,b; Reilly et al., 2013). Due to specialized diets and foraging strategies that entail long-distance trips to find dense patches of euphausiids to achieve sufficient foraging efficiency, these three species of whales (hereafter "rorqual whales") may have a lower capacity for adaptation and therefore are more vulnerable to human-induced changes in the marine environment than other species (Trathan et al., 2007; Kovacks and Lydersen, 2008). The fluctuations in the use of habitat of rorqual whales is mostly determined by multiple

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oceanographic variables and their effects on prey distribution and abundance (Croll et al., 2005; Doniol-Valcroze et al., 2007; Gill et al., 2011). Environmental conditions that allow for high concentrations of rorqual whales' prey occur in coastal zones, upwelling areas, fronts, seamounts, and offshore regions of high marine productivity (Croll et al., 2005; Johnston et al., 2005; Doniol-Valcroze et al., 2007; Gill et al., 2011; Visser et al., 2011). Even though these highly productive areas are characterized by a high human pressure, few studies have included both environmental and anthropogenic stressors (such as the presence of fisheries) in the habitat models.

This lack of information is clearly evident along the North-western Iberian coast (Spain), region renowned for having been a whaling area of significance (Sanpera and Aguilar, 1992), and where global warming might lead to a decrease in upwelling intensity (Álvarez et al., 2008; Pérez et al., 2010; Santos et al., 2011; Miranda et al., 2013; Casabella et al., 2014). The different marine predator species present along this highly productive locus of intensive fisheries and important marine traffic area, are also vulnerable to a number of direct human impacts such as marine traffic, by-catch, overfishing, oil spill, and habitat modification (Freire and García-Allut, 2000; López et al., 2003; Vieites et al., 2004; Díaz López and Methion, 2018).

In this study, we predicted that rorqual whales should adjust their fine-scale movements in response to the local availability of resources associated to upwelling episodes. We tested this hypothesis through a comprehensive investigation of the key environmental and anthropogenic correlates of habitat use and relative density of aggregations of blue, fin and sei whales in this highly impacted coastal region (North-western Iberian coast, Spain). As such, investigating fine-scale fluctuations in habitat utilization is essential for a better understanding of the response of these species to human-induced changes in coastal upwelling systems. This information can therefore be used as a relevant indicator of the degree of vulnerability of endangered rorquals to human-induced changes providing comprehensive information on which to base conservation and adaptive management strategies.

2. Methods

2.1. Study area

The present study was performed along the North-western coast of the Iberian Peninsula, more particularly along the southern coast of Galicia (Spain), covering the entire continental shelf from Muros (42.79° N, 9.15° W) to Cíes Islands (42.36° N, 8.94° W) (Fig. 1). The study area encompassed 1 300 km^2, with 92% of the area corresponding to the continental shelf (depth < 200 m) and the rest covering the continental slope down to a depth of 1 050 m.

The southern coast of Galicia is at the northern boundary of the North Atlantic Upwelling System, one of the four major upwelling systems in the world (Pérez et al., 2010). Oceanographic patterns in the region are modulated by the seasonal cycle of the wind direction, where the prevalence of North-eastern winds during spring-summer months is the main cause of coastal upwelling events that significantly increases primary production (Álvarez et al., 2011). Recent estimations indicate that both the strength of the upwelling events and the length of the upwelling season have changed significantly over the second half of the 20th century (Álvarez et al., 2008; Pérez et al., 2010; Santos et al., 2011; Miranda et al., 2013; Casabella et al., 2014).

2.2. Data collection

A 12 m fly-bridge research vessel "Tyba III" was used to systematically monitor the study area, recording data on presence and behaviour of rorqual whales, and oceanographic variables. Boat-based observation surveys were carried out year-round from January 2016 until November 2017, monitoring the area with systematic transect lines adapted to match the specific conditions of the study area. The study area was surveyed during daylight hours at a continuous speed between 6 and 8 knots, with at least three experienced observers, stationed on the flying bridge (situated at 4 m above the sea level), scanning 360 degrees of the sea surface in search of whales (with the naked eye and 10 × 50 binoculars). The spatial distribution of the effort varied according to weather conditions and time constraints throughout the study period. Surveys were done when the sea conditions were up to 4 on the Beaufort wind force scale, wave height smaller than 1.5 m, and visibility was not reduced by rain or fog.

On each survey, the time, position, vessel speed, presence of rorqual whales (within a 1 nm radius of the boat's position), anthropogenic and environmental data were recorded as an instantaneous point sample every 20 min. These instantaneous samples were used to summarize field conditions and distribution of the effort from the beginning until the end of each survey, irrespective of whales' presence. The spatial resolution of this 20 min interval was approximately 2 nm (given a 6–8

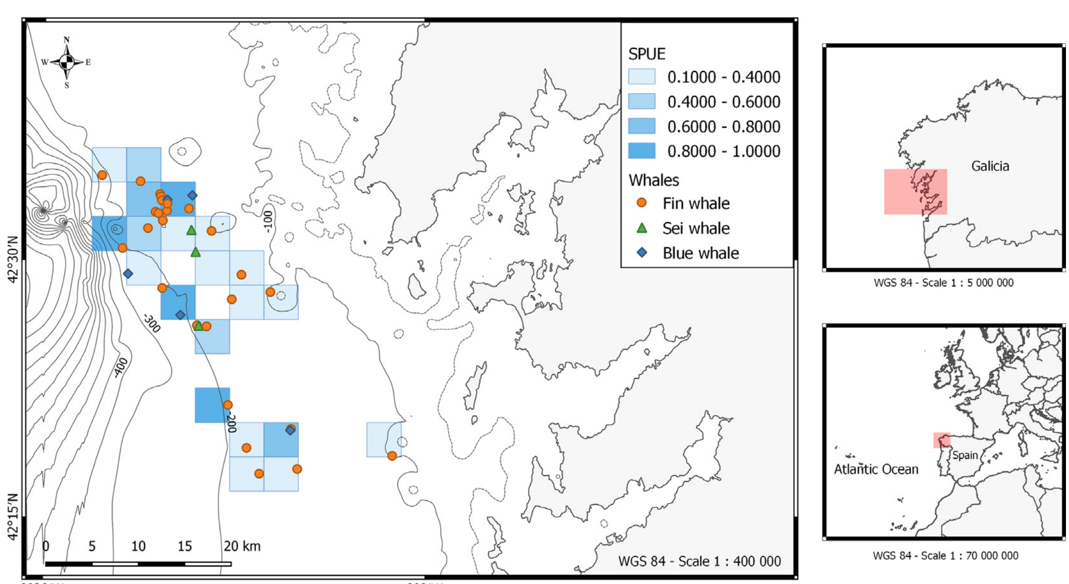

Fig. 1. Map of the study area surveyed along the Northwestern coast of Spain, showing the distribution of the three species of endangered rorqual whales. The grid corresponds to the distribution of rorqual aggregations corrected for search effort within each 2 nm^2 cell (SPUE).

kt speed) (Díaz López and Methion, 2018) and the visual detection/non-detection of whales was recorded instantaneously for all the 20 min sampling points. Upon sighting of rorqual whales, searching effort ceased and the vessel slowly manoeuvred towards the whales in order to minimise disturbance during the approach. An aggregation of rorqual whales was defined as one or more whales of at least one of the three endangered species (blue whale, fin whale, or sei whale), observed within a 1 nm radius. Because the research vessel often stayed with the animals, whales could be observed at close ranges (< 50 m) and for long periods of time (> 45 min). Digital photographs of the body and dorsal fin of rorqual whales were taken using a digital single lens reflex (DSLR) camera equipped with a 18- to 300- mm and a 200- to 500- mm telephoto zoom lens. At the end of a sighting, the searching effort continued along the previously planned route.

Fourteen predictors were selected according to data availability for each 20 min sample recorded during the study and biological relevance to the factors that could potentially affect the rorqual whales' use of habitat based upon previous investigation of the literature (Croll et al., 2005; Johnston et al., 2005; Doniol-Valcroze et al., 2007; Gill et al., 2011; Visser et al., 2011). Thirteen environmental variables: date, time (UTC, in hours), position (coordinates), depth (m), bottom slope gradient (expressed as percent slope), bottom slope aspect (the orientation of the slope with respect to true north), tide level (m), tide cycle (rising with the flooding tide and falling with the ebbing tide), sea surface temperature (SST in ° Celsius), distance to the coast (m), wind speed (m/s), chlorophyll *a* (CHL-a in mg/m^3), and upwelling index (m^3/s × km). One anthropogenic variable, number of fishing vessels within a 1 nm visual range, was also considered.

The date, time, position, depth, and SST were obtained by a GPS-Plotter Map Sounder associated with an 83–200 kHz echo-sounder transducer. The wind speed (as an associated measure of sea state) was measured when the vessel was stationary (one minute at the beginning of each 20 min point sample) by a cup anemometer situated 4 m above the sea level. Tide level (m) and tidal cycle (presence/absence of flood tide) were obtained for the harbour of Ribeira from the Galician weather service (http://www.meteogalicia.gal). Bottom slope gradient and slope aspect, were computed from the bottom depth obtained from a bathymetric chart data set, with a 500 m × 500 m resolution, digitized from two 1 : 50 000 scale nautical charts from the Instituto Hidrográfico de la Marina (Spain). This dataset was converted to a raster format and then interpolated using QGIS software (www.qgis.org) terrain analysis tools. All distances to the coast were minimum distances in metres from the GPS position of each 20 min sample to the perimeter of the shoreline and calculated via spatial analyst tools using QGIS software (Díaz López and Methion, 2018). Chlorophyll-a data were obtained as daily rasters, with a spatial resolution of 1 km × 1 km, for the position of each 20 min sample from the COPERNICUS Marine Environment Monitoring Service website (http://marine.copernicus.eu). Upwelling index (Bakun, 1973) was obtained from the Instituto Español de Oceanografía (http://www.indicedeafloramiento.ieo.es) and was calculated using sea level pressure of the Meteogalicia WRF atmospheric model.

2.3. Data analysis and modelling framework

Overall, 711 samples were collected instantaneously every 20 min of which 542 were searching for whales (on-effort data). All samples collected in waters deeper than 600 m were excluded for further analysis because there were unrepresented in the study (n = 4 samples). A data set was generated by randomly selecting 250 samples searching for whales (35% of the total samples). By down-sampling the on-effort data the lack of independence arising from consecutive samplings was limited, avoiding the influence of variations in the observation effort, and limiting pseudo-replication (Díaz López and Methion, 2018).

Date was not included as covariate, because it was related with environmental variables that show seasonal changes (i.e. sea-surface temperature, Chlorophyll-a, and Upwelling index) which were included instead due to their biological interpretability (Forney, 2000), and to prevent over-parameterization (Burnham and Anderson, 2002). Likewise, latitude and longitude were not included in further analysis, because they were highly correlated with water depth and distance to the coast (Spearman rho > 0.75, $p < 0.01$).

Generalized additive models (GAMs, Hastie and Tibshirani, 1990) were used to explore the variables that might have affected the distribution of blue, fin and sei whales. A GAM is a non-parametric generalization of multiple linear regressions, widely-used for interpreting ecological interactions and is particularly well-suited for the type of non-linear responses that are expected in species-environment relationships (Hastie and Tibshirani, 1990). The GAMs results and diagnostic information about the fitting procedure were implemented from the mgcv package (Wood, 2006) in v. 1.8.1. of the statistics and graphics tool R (R Development Core Team, 2011). Data exploration protocols described by Zuur et al. (2010) were used to identify outliers, data variability, and relationships between predictors and the presence of rorqual whales (response variable). Modelling was initiated using a basic GLM to assess multicollinearity (Zuur, 2012) by examining the variance inflation factor (VIF); when VIF > 5, the variable was omitted (Dormann et al., 2013). Following this procedure, distance to the coast was excluded from further analyses.

Presence-absence of rorqual whales was modelled as a binomial GAM with a logistic link function and the smooth functions were represented by cubic regression splines (Wood, 2006). For all continuous explanatory variables, smoothers were constrained to a maximum of 4 degrees of freedom, except for wind speed and Upwelling index (with a maximum of 6 degrees of freedom), thus limiting relationships to plausible simple forms and avoiding overfitting. Model assumptions were checked by visual inspection of the residuals and regression fits were examined using plots of residuals against fitted values. The Durbin-Watson test (from the package “lmtest” (Zeileis and Hothorn, 2002)) and auto-correlation functions (ACF) were used to check for serial correlation, both in our raw data and in the residuals from the models. The optimum final model (hereafter referred to as global model) was selected based on the lowest Unbiased Risk Estimator (UBRE) and there were no clear patterns in the residuals (Hastie and Tibshirani, 1990).

Because of the large number of potential combinations of predictor variables, model simplification and selection were done following a multi-model inference approach (Burnham and Anderson, 2002; Grueber et al., 2011). The R package ‘MuMIn’ (Barton, 2011) was used to produce a candidate model set consisting of all simplified versions of the global model and compared them based on their AIC corrected for small sample sizes (AICc) (Grueber et al., 2011). To ensure that the most parsimonious models were maintained within the best supported model set, the models with Δ AICc < 2 were selected to identify the relative importance of each model term in predicting the response variable and to estimate the effect sizes of the predictors (Burnham and Anderson, 2002). Ecological conclusions were drawn from the direct comparison of this set of models that provided substantial support. Models were ranked from best to worst using the difference in AICc between the particular model and the first-ranked model (Δi) ((Δi = AICc(i) − AICc(min)) and the Akaike weights (wi) were calculated to give the relative support for a given model compared with the others (Grueber et al., 2011). Furthermore, the relative importance of a predictor variable (RVI) was calculated as the sum of the Akaike weights overall of the models in which the predictor appears (Burnham and Anderson, 2002). Partial predictions with 95% confidence intervals were plotted for each covariate included within the best supported model set. The data are presented as means ± standard error (s.e.).

3. Results

3.1. Survey effort and presence of rorqual whales

The field effort spanned over two consecutive years of fieldwork from January 2016 to November 2017. In total, 32 daily boat surveys within 12 different months were spent in the field covering 2 925 km. A total of 250 h were spent in adequate weather conditions (mean = 8 ± 0.6 h per day) and the total distance covered in a day was up to 170 km (mean = 98 ± 7 km). Throughout this period 54 rorqual whales were spotted on 29% of the total number of daily surveys (Fig. 1). Rorqual whales were spotted with a mean first cue distance of 580 ± 88 m (median = 400 m, min = 30 m, max = 2 000 m). The size of the aggregations ranged from 1 to 12 individuals (mean = 3.1 ± 0.4 individuals, n = 34) and were monitored for a total of 19 h. Solitary rorqual whales were seen in 21% of the encounters (6 solitary fin whales and 1 solitary blue whale). Most of the encounters (79%) corresponded to intra or interspecific aggregations of rorqual whales. There were 18 aggregations of fin whales, 4 interspecific aggregations with fin and blue whales, 3 interspecific aggregations with fin and sei whales, and 2 interspecific aggregations with all three species (fin whales, blue whales, and sei whales). Overall, 23 individuals, with recognizable marks in their dorsal fins, were photo-identified (17 fin whales, 4 sei whales, and 2 blue whales). The sighting frequency of these photo-identified individuals ranged from 1 to 4 encounters across the duration of the study. Particularly 2 fin whales and 1 blue whale, accounting for 13% of all identified individuals, were identified in more than one different day throughout the study period. Of these individuals, 1 fin whale and 1 blue whale were observed over a period of 52 and 21 days, respectively.

Evidence of foraging activities was confirmed in 66% of the encounters with the observation of euphausiid surface swarms at the surface or underwater observation of whales with partly open mouths and distended throat pouches. Surface swarms of northern krill (*Meganyctiphanes norvegica*) were observed in a range of bottom depths between 100 and 250 m, although rarely exceeding 250 m. Additional sightings of other species of whales in the area included 10 encounters with minke whales (*Balaenoptera acutorostrata*) and 2 encounters with humpback whales (*Megaptera novaengliae*). These two species of whales were never seen in aggregation with fin, blue and sei whales.

3.2. Environmental and anthropogenic correlates of rorqual whales' presence

A global GAM was created with 10 selected environmental and anthropogenic variables that did not contain collinearity: time of the day, SST, CHL-a, Upwelling index, tidal cycle, depth, slope, aspect, number of fishing boats, and wind speed. The global model explained around 61.1% of the variation in the data (R-sq = 0.556, UBRE = -0.519, AICc = 124.1). A candidate model set consisting of 1 024 simplified versions of the global model was produced. Afterwards, the simplified versions were compared based on their AICc and only nine top models with Δ AICc < 2 were used to produce model averaged parameter estimates (Table 1).

Variables as depth, bottom slope aspect, SST, Upwelling index, and wind speed were all retained in each model within the candidate model set having a relative variable importance (RVI) of 1 in the final average model (Table 2). Time of the day was retained in 7 models and had a RVI of 0.75. Tidal cycle was retained in 6 of the top models and had a RVI of 0.73. Number of fishing vessels, bottom slope gradient and CHL-a concentration were retained in only 2 models and had a relative variable importance (RVI) of 0.30, 0.17 and 0.15 in the final averaged model, respectively.

Rorqual whales' occurrence was predicted to be more likely at the edge of the continental slope (200 m depth, strong bottom slope gradient with a south-western facing aspect), during the first hours of the day, under moderate upwelling conditions, cold sea surface water temperatures (< 16° Celsius), and with a reduced number of fishing vessels (Table 2, Fig. 2).

Table 1
Most likely models explaining the variation in presence of aggregations of rorqual whales in relation to environmental and anthropogenic variables. Depth, CHL = concentration of chlorophyll-a, Wind = wind speed, SST = sea surface temperature, Slope = bottom slope gradient, Tide = tidal cycle, Asp = bottom slope aspect, Boats = number of fishing vessels, UI = Upwelling index, time = hour of the day.

Model	Df	logLik	AICc	Δi	wi
Depth/Asp/time/SST/UI/Wind/Tide/	17.41	−41.13	119.84	0.00	0.18
Depth/Asp/Boats/SST/UI/Wind/Tide/	17.12	−41.55	120.02	0.18	0.17
Depth/Asp/time/Boats/SST/UI/Wind/Tide/	18.36	−40.38	120.56	0.73	0.13
Depth/Asp/time/SST/UI/Wind/	16.20	−42.91	120.63	0.80	0.12
Depth/Asp/time/SST/Slope/UI/Wind/Tide/	18.46	−40.59	121.21	1.37	0.09
Depth/Asp/time/CHL/SST/UI/Wind/Tide/	18.66	−40.50	121.50	1.66	0.08
Depth/Asp/SST/UI/Wind/Tide/	16.25	−43.32	121.54	1.70	0.08
Depth/Asp/time/CHL/SST/UI/Wind/	17.44	−42.01	121.68	1.84	0.07
Depth/Asp/time/SST/Slope/UI/Wind/	17.22	−42.26	121.68	1.84	0.07

Only nine most candidate models (Δi ≤ 2) of the 1024 are presented, df degrees of freedom, Δi difference between the particular model and the best model, wi Akaike weight showing the relative support of a given model compared to the others.

4. Discussion

One of the critical challenges facing ecologists is understanding how endangered marine predator species respond to anthropogenically-induced changes in the environment, and which regions and species will be most impacted by these changes (Pauly et al., 2005; Read et al., 2006; Halpern et al., 2007; Hoegh-Guldberg and Bruno, 2010). This study contributes to extend the scant information available about the distribution of blue whales, fin whales and sei whales in the North-east Atlantic (Pike et al., 2009; Víkingsson et al., 2009). The continental shelf in Galician waters is a highly impacted coastal region frequently utilized as a foraging area by these endangered rorquals. The unequal use of available habitat, concentrated at the edge of the continental slope in areas with a south-easterly coastal orientation, showed that rorqual whales presented a fine-scale pattern of habitat selection. Of the investigated non-persistent environmental factors, sea surface water temperature and Upwelling index appeared to have a clear effect in the occurrence of rorqual whales in the region. These stressors are directly affected by the coastal upwelling regime of the Iberian Peninsula (Gómez-Gesteira et al., 2008), which is known to be under the impact of climate change (Álvarez et al., 2008; Pérez et al., 2010; Santos et al., 2011; Miranda et al., 2013; Casabella et al., 2014). Likewise, the south-easterly coastal orientation, characteristic of the zones preferred by rorqual whales, modulates wind direction and intensity facilitating the upwelling favourable conditions prevalence (Torres et al., 2003; Álvarez et al., 2011).

The observed link between the most relevant environmental predictors related to upwelling episodes and rorqual whales' presence does not necessarily imply a direct relationship. Thus, variability in rorqual whales' responses to the correlates is likely a result of the complex and dynamic interactions of these factors with prey availability (Friedlaender and Goldbogen, 2015). Since these three species need dense aggregations of euphausiids such as the northern krill to enable efficient foraging (Whitehead and Carscadden, 1985; Friedlaender et al., 2006), their presence will not coincide with the timing of strong upwelling episodes. Upwelling favourable northerly winds (predominant during spring and summer months) are responsible of forcing the uplift of cold waters at the edge of the continental slope bringing

Table 2
Examples of the predicted effect of each variable included in the model-averaged model on the presence of rorqual whales, with the other predictors held at their mean (N = 250). RVI = relative variable importance, N models = number of containing models. Aspect = bottom slope aspect, Slope = bottom slope gradient, SST = sea surface temperature, CHL-a = concentration of chlorophyll-a, Boats = number of fishing vessels, UI = Upwelling index.

Predictor		Estimated presence (%) of endangered rorquals	RVI	N models
Depth	50 m	0.0 ± 0.0	1	9
	100 m	2.1 ± 3.5		
	200 m	97.2 ± 3.6		
	400 m	0.1 ± 0.8		
Wind speed	0 m/s	1.1 ± 2.2	1	9
	2 m/s	1.5 ± 2.7		
	4 m/s	1.7 ± 3.4		
	6 m/s	0.0 ± 0.0		
UI	$-1500\ m^3 \times s^{-1} \times km^{-1}$	3.0 ± 6.1	1	9
	$-500\ m^3 \times s^{-1} \times km^{-1}$	2.0 ± 3.7		
	$500\ m^3 \times s^{-1} \times km^{-1}$	10.4 ± 17		
	$1500\ m^3 \times s^{-1} \times km^{-1}$	0.0 ± 0.0		
Aspect	North-eastern facing (45°)	0.0 ± 0.0	1	9
	South-eastern facing (125°)	1.0 ± 1.9		
	South-western facing (225°)	1.7 ± 3.0		
	North-western facing (315°)	0.2 ± 0.5		
SST	13° Celsius	52 ± 56	1	9
	14° Celsius	24 ± 37		
	16° Celsius	2.8 ± 5.0		
	18° Celsius	2.6 ± 0.5		
Time	6.00 h	9.3 ± 16	0.75	7
	10.00 h	3.4 ± 6.0		
	14.00 h	1.2 ± 2.1		
	18.00 h	0.4 ± 0.8		
Tidal cycle	Flood	0.8 ± 1.6	0.73	6
	Ebb	2.4 ± 4.3		
Boats	0	4.0 ± 5.9	0.30	2
	10	1.3 ± 2.0		
	20	0.4 ± 0.8		
Slope	0°	1.2 ± 2.3	0.17	2
	10°	2.5 ± 5.0		
	15°	3.6 ± 7.6		
	20°	5.1 ± 11.8		
CHL-a	0.5 mg/m3	0.1 ± 0.2	0.15	2
	2 mg/m3	0.2 ± 0.4		
	6 mg/m3	0.9 ± 0.2		
	12 mg/m3	9.0 ± 30		

nutrient-rich waters from the lower depths (Álvarez et al., 2008). These conditions facilitate the patchy but dense, ephemeral aggregation of primary producers in particular zones where the frequency and intensity of upwelling events are influenced by coastal orientation (Bode et al., 2009). Coastal upwelling occurs as pulses of maximum intensity, with a frequency of 10 to 20 days, separated by intermediate periods of less upwelling-favourable winds (Álvarez-Salgado et al., 2002; Otero et al., 2009). Given the characteristics of the upwelling events along this coastal region, the phytoplankton bloom is also a discontinuous process with maximum abundances appearing in various pulses (Bode et al., 2009). The development of euphausiids, to become prey of rorqual whales, follows the phytoplankton bloom with a time lag of several weeks (Visser et al., 2011). This supports the existence of a discrete time lag between the peak upwelling favourable conditions and the presence of rorqual whales in the area. Findings of this study represent the fact that higher wind speeds make it less likely to find rorqual whales on a daily scale rather than wind acting on upwelling processes at a longer scale.

This study shows that rorqual whales likely adjust their movements at finer spatial scales to find individual prey patches. The observation of rorqual whales feeding during several consecutive weeks reinforces the existence of dense aggregations of euphausiids in these waters. Rorqual whales demonstrate temporal synchrony with their prey (primarily euphausiids) and their migratory behaviour is related to temporal heterogeneity in ocean productivity. One blue whale (Supplementary Material: Photo 1) and one fin whale observed during the study in September-October 2017 were previously sighted in Azores islands two months before (Lisa Steiner and Richard Sears, pers. communication) suggesting that rorqual whales might originate from southerly grounds with a northward feeding migration pattern from July to October.

This study provides relevant information to assess the vulnerability of endangered species of rorqual whales to human-induced changes in this highly productive coastal environment. A decrease in upwelling intensity in this region could induce fluctuations in timing annually recurring events (phenology) and a decrease in prey availability for these endangered species of rorqual whales. Responses of rorqual whales to upwelling changes might be manifested at the population level such as shifts in abundance and distribution. Likewise, the decline of coastal upwelling off North-western Iberian Peninsula was linked with the decline in zooplanktivorous fish species such as sardines (*Sardina pilchardus*) (Pérez et al., 2010), that present the same northward feeding migration pattern as rorqual whales (Carrera and Porteiro, 2003).

On the other hand, these highly productive waters are subject to significant use by humans including fisheries and important marine traffic (Vieites et al., 2004; Díaz López and Methion, 2018). Our findings show what appears to be rorqual whales' avoidance behaviour in response to fishing vessels as the occurrence of whales tended to decrease with a higher number of fishing vessels (characterized mostly by bottom trawlers). These results are consistent with behavioural responses of blue whales to oncoming ships to avoid collision observed off the coast of southern California (McKenna et al., 2015). Unfortunately, there is a lack of information about ship-whale collisions in the region. Deaths of rorqual whales have been documented for stranded whales mostly with injuries indicative of entanglement in fishing gear (López et al., 2003). Indeed, a fin whale with a fishing net (from bottom set trawling) caught around its head was observed during this study (Supplementary Material: Photo 2). The consequences of fisheries on marine food web may also require special attention where a resource base like marine grazers, is likely to decrease under climate variations in the region (Pérez et al., 2010). These observations support the assumption that with an increase of 16% of the bottom set trawling catches along the continental shelf in the last 10 years (official catches from Ribeira harbour, Galician Institute for Statistics, 2018), current harvesting regimes along the study area might impact, directly or indirectly, on the survival of these endangered species in the region. As future climate scenarios predict a decline in krill populations due to changes in upwelling intensity, the fisheries sector will need to adjust harvesting to minimise the impact on community composition and trophic structure and to ensure resources are not overexploited.

Findings of this study provide management agencies with an opportunity to devise and implement initiatives which will contribute towards the continued survival of rorqual whales in the region. Moreover, these results may help concentrate conservation efforts primarily on the areas of highest concern. A broad spectrum of potential adaptation strategies, ranging from a reduction of significant bottom trawl fisheries in this area, marine traffic regulations, and by adequate whale-watching activities (which is as yet undeveloped), may ameliorate adverse effects critical for the conservation of these endangered marine predators in a changing climate.

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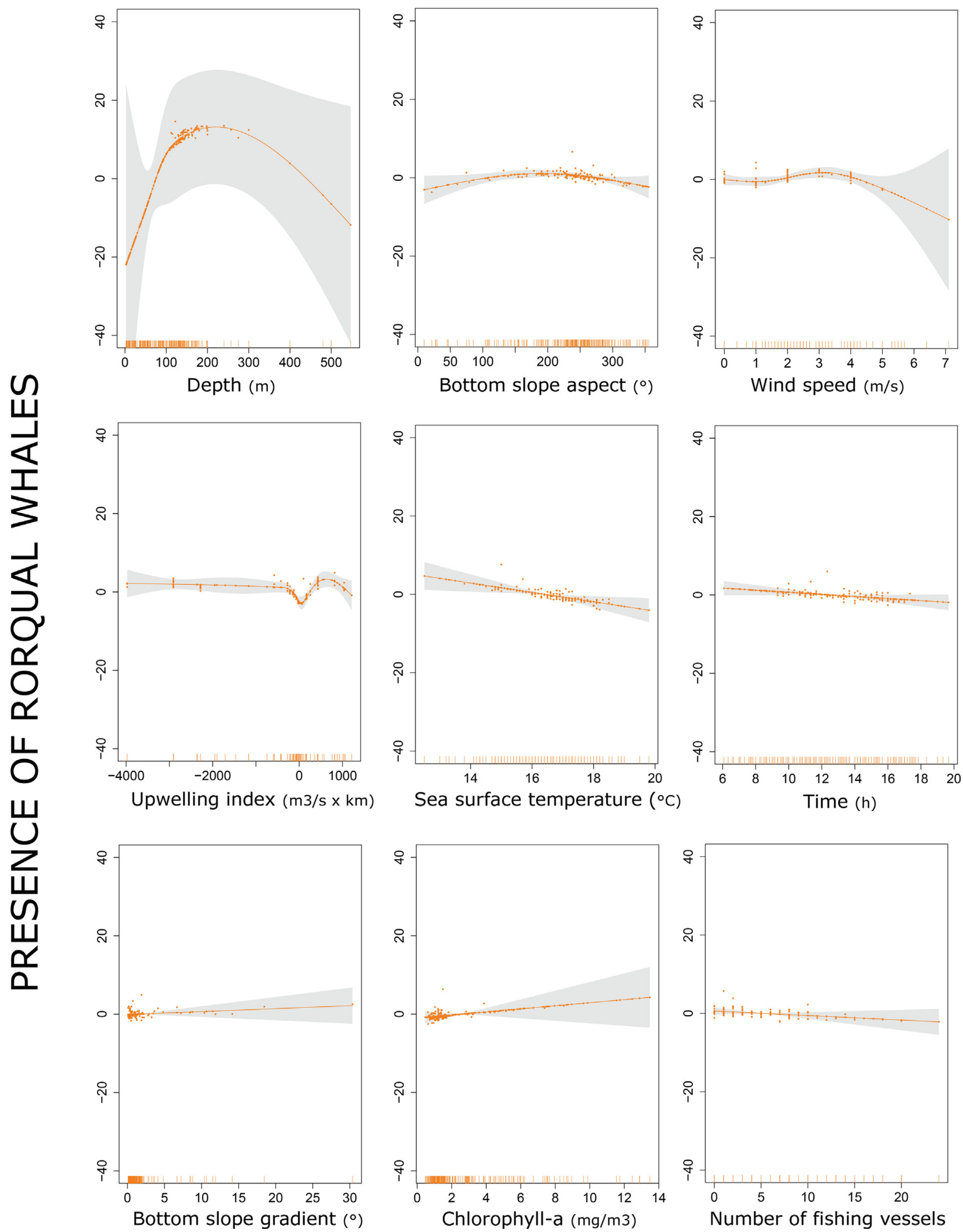

Fig. 2. Averaged predictions of rorqual whales presence for each covariate present in the confidence set of models and their 95% confidence limits when all other variables are fixed to their mean value.

regarding the blue whale and fin whale photo-identified in Azores (Portugal). We wish to thank the very helpful comments and editing provided by João Carlos Marques and two anonymous reviewers. Many thanks are also extended to the BDRI students and volunteers who assisted with fieldwork and data transcription. Data collection complies with the current laws of Spain, the country in which it was performed.

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Conflict of interest

The authors of this study declare that they have no conflict of interest.

Author Contributions: B.D.L. conceived the study. B.D.L and S.M. collected the data and discussed the results of the study. B.D.L analysed data and wrote the paper with input from S.M.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2019.04.038.

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